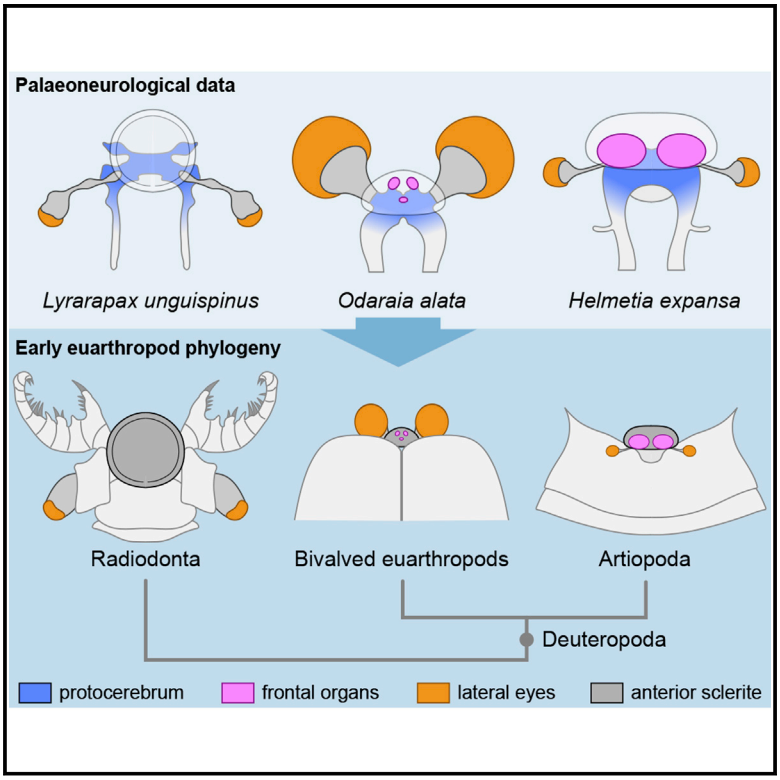
Report

Current Biology

Homology of Head Sclerites in Burgess Shale Euarthropods

Graphical Abstract



Highlights

- Neurological remains are described for (middle Cambrian) Burgess Shale euarthropods
- Preserved frontal organs and lateral eyes show connections with anterior brain region
- The anterior sclerite in stem-group Euarthropoda is associated with the protocerebrum
- The euarthropod anterior sclerite is homologous to the radiodontan dorsal plate

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In Brief

Ortega-Hernández demonstrates that the anterior sclerite, an enigmatic structure in the head region of Cambrian euarthropods, is associated with the protocerebral segment based on exceptionally preserved neurological remains in Burgess Shale fossils. The origin of the anterior sclerite precedes the evolution of the multisegmented euarthropod head.

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Current Biology
Report

Homology of Head Sclerites in Burgess Shale Euarthropods

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SUMMARY

The Cambrian fossil record of euarthropods (extant arachnids, myriapods, crustaceans, hexapods) has played a major role in understanding the origins of these successful animals and indicates that early ancestors underwent an evolutionary transition from soft-bodied taxa (lobopodians) to more familiar sclerotized forms with jointed appendages [1–3]. Recent advances in paleoneurology and developmental biology show that this major transformation is reflected by substantial changes in the head region of early euarthropods, as informed by the segmental affinity of the cephalic appendages [1, 4–6]. However, data on the implications of this reorganization for non-appendicular exoskeletal structures are lacking, given the difficulty of inferring the precise segmental affinities of these features. Here, I report neurological remains associated with the stalked eyes and ''anterior sclerite'' in the (middle Cambrian) Burgess Shale euarthropods *Helmetia expansa* and *Odaraia alata* and provide evidence that these features are associated with nerve traces originating from the anterior brain region, the protocerebrum. The position of the protocerebral ganglia in exceptionally preserved Cambrian euarthropods indicates the homology of the anterior sclerite in extinct groups (e.g., fuxianhuiids, bivalved forms, artiopodans [7, 8]) and allows new comparisons with the dorsal cephalic plate of radiodontans, large nektonic predators whose anterior segmental organization bears fundamental similarities to that of Paleozoic lobopodians [1, 6, 9, 10]. These observations allow reconstruction of the segmental architecture of the head region in the earliest sclerotized euarthropods and demonstrate the deep homology between exoskeletal features in an evolutionary continuum of taxa with distinct types of body organization.

RESULTS AND DISCUSSION

The ''(eu)arthropod head problem'' refers to the complications of comparing the anterior segmentation between phylogenetically and morphologically disparate representatives within this successful group [11, 12]. Recent studies have clarified the homology of head segments in extant euarthropods [12–16], leading to a substantial understanding of the anterior appendage organization in various phylogenetically basal fossil taxa [1, 2, 4–7, 12]. However, there are major issues regarding the early evolution of Paleozoic euarthropods that remain unresolved. Although it is widely accepted that stem-group Euarthropoda includes disparate forms characterized by either a lobopodian-type (lower stem euarthropods) or a completely sclerotized body architecture (upper stem euarthropods), the precise segmental reorganization of the head involved in this evolutionary transition is less resolved [1, 2, 11, 12]. Developmental and paleontological evidence support the pre-ocular origin of the raptorial ''frontal appendages'' of radiodontans [6, 9, 10, 17, 18], as well as their homology with the euarthropod labrum [2, 3, 7, 13, 15] (see Supplemental Discussion). By contrast, the segmental affinity of non-appendicular exoskeletal structures in the head remains enigmatic given the difficulties of testing their homology across the transition from lower to upper stem-group Euarthropoda [1] (Table S1).

The head of several Paleozoic euarthropods bears an ''anterior sclerite'' [8, 19] (alternatively ''prehypostomal sclerite'' [20, 21]), a cuticular plate that articulates with the anteriormost portion of the dorsal exoskeleton (Figures 1 and 2), including fuxianhuiids [7, 22–25], bivalved stem euarthropods [8, 26, 27], and artiopodans [19, 21, 28–31] (Table S2). Despite its ubiquitous nature, the significance of the anterior sclerite remains controversial, as there is little agreement on the correspondence of this structure among stem- and crown-group euarthropods [8–10, 20, 21, 25, 28, 32] (Table S1). Examinations of the cephalic region in the (middle Cambrian) Burgess Shale euarthropods *Helmetia expansa* and *Odaraia alata* reveal the preservation of nervous tissues, cast new light on the segmental origin of the anterior sclerite, and elucidate its homology within total-group Euarthropoda (Figures 3 and 4). This study contributes significantly to an emerging body of evidence demonstrating the exceptional preservation of delicate neurological structures [4–7, 38, 39] in Burgess Shale-type deposits [35, 36, 40].

The following institutional abbreviations are used herein: ELRC, Early Life Research Centre, Nanjing Institute of Geology and Paleontology, Nanjing, China; ROM, Royal Ontario Museum, Toronto, Canada; USNM, National Museum of Natural History, Washington, DC, USA; YKLP, Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming, China.

Frontal Organs in *Helmetia expansa*

H. expansa bears a prominent (~33% cephalic width, transverse; 25% cephalic length, sagittal) semicircular anterior sclerite (*asc* in Figures 1 and 4D; see also Figures S1 and S2) that narrowly

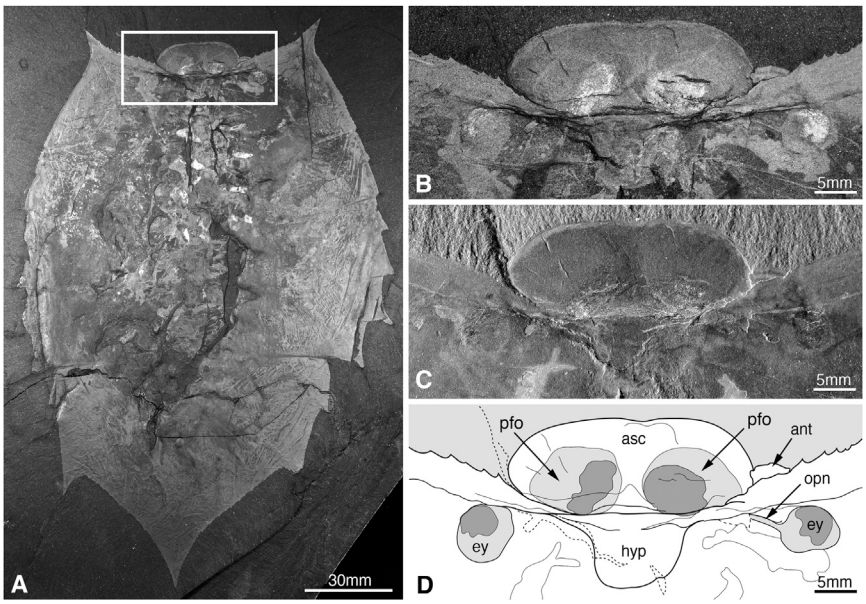

Figure 1. Protocerebral Structures in *Helmetia expansa*

(A) Holotype (USNM 83952) in dorsal view (cross-polarized high-angle illumination, dry). White box indicates location of magnified area in (B)–(D).

(B) Detail of anterior cephalic structures (cross-polarized high-angle illumination, dry).

(C) Detail of anterior cephalic structures (cross-polarized low-angle illumination, dry).

(D) Interpretative line drawing of USNM 83952. Grayscale indicates different styles of preservation: white, non-reflective cuticle; light gray, mildly reflective neurological structures; dark gray, highly reflective neurological structures. Dotted lines indicate non-biological fissures. Note that the morphology of the optic nerve (*opn*) reflects that of the eyestalk, and thus only the former is labeled in the figure. Other abbreviations used: *ant*, antenna; *asc*, anterior sclerite; *ey*, eyes; *hyp*, hypostome; *pfo*, protocerebral frontal organ.

overlaps with a comparatively smaller subtrapezoidal hypostome [8, 19]. The anterior sclerite is accommodated within a notch on the anterior cephalic margin, as typical for most members of Conciliterga, non-biomineralized euarthropods closely related to trilobites and characterized by diverse patterns of exoskeletal tagmosis [19, 23, 29–31] (see Table S2; Figure S1). The holotype of *H. expansa* (USNM 83952) evinces large (~40% anterior sclerite, transverse; 66% anterior sclerite, sagittal) and paired highly reflective subcircular structures within the anterior sclerite, the frontal organs (see *pfo* in Figures 1B–1D and 4D), situated immediately anterior to the articulation of the former with the cephalic notch. The frontal organs are preserved as flattened compressions and display a bright silver hue under reflected light (Figure 1B; see also Figures S1, S2A, and S2B), which contrasts with the more opaque appearance of the adjacent cuticle; such attributes indicate that these features are preserved as graphitized carbonaceous films, as documented for Burgess Shale fossils [35, 40]. Each frontal organ displays an area of higher reflectivity close to the body midline, mirroring differences in preservation and original histology. The frontal organs are indistinguishable from the overlying cuticle under low-angle illumination, except for a subtle convexity expressed on the anterior sclerite, indicating that they represent ventral structures (Figure 1C). The absence of associated stalks and their consistent position in the body (Figures S1 and S2B) indicate that the frontal organs are sessile and firmly attached to the underside of the anterior sclerite. Anteriorly, USNM 83952 shows the preservation of two lateral eyes (see *ey* in Figures 1B–1D and 4D; see also Figures S1, S2A, and S2B) on the ventral side—confined to elevated bulges on the dorsal side of the cephalon [19, 29–31]—that are connected to the frontal organs by delicate eyestalks (see *opn* in Figure 1D); only the right stalk is fully visible. The preservation of the stalked eyes as highly reflective films is identical to that of the frontal organs, suggesting a similar original histology (Figures S1 and S2). There is no evidence for the preservation of either lenses or ommatidia.

The frontal organs of *H. expansa* have been regarded as possible median eyes [8, 19]—a view favored in this study—and thus likely had a photoreceptive function [33, 34, 37, 41–44]; the same interpretation has also been invoked for similar paired structures on the anterior sclerite of other conciliterga [19], or alternatively in close association with the hypostome/labrum complex in other artiopodan groups [23, 28] (Table S2). The association between the stalked lateral eyes and the frontal organs in *H. expansa* (Figures 1B and 1D; see also Figure S1) and their similar preservation and position in the cephalon suggest that these features originate from the anterior region of the brain. Indeed, both the median and lateral eyes of extant euarthropods derive from the protocerebrum, despite significant diversity in their structural organization (e.g., presence versus absence of optic neuropils in median eyes of Chelicerata and Mandibulata respectively) and precise innervation relative to the brain neuropils [33, 34, 37, 41–44] (see Figures 4E and 4F). The topological correspondence of the frontal organs with the lateral eyes and the anterior sclerite of *H. expansa* provide strong evidence that the latter exoskeletal feature has a fundamental association with the protocerebral segment.

Brain Structure in *Odaraia alata*

O. alata possesses a relatively small and subtriangular anterior sclerite at the front end of the body, adjacent to the bivalved carapace (see *asc* in Figure 2; see also Figures S2C–S2E and S3) [8]. The anterior sclerite is flanked by a pair of large (~150% anterior sclerite, transverse and sagittal) lateral eyes that attach to former structure through robust stalks (see *opn* in Figures 2B–2D). The lateral eyes are preserved as highly reflective carbon films (Figure 2; see also Figures S2 and S3); ROM 60746 suggests detail of individual ommatidia (Figure 2B), but this interpretation is inconclusive [45]. High-angle illumination reveals internal details—preserved as reflective films—within the anterior sclerite of *O. alata.* ROM 60746 (Figures 2B and 2D) and USNM 189232 (Figures 2E and 2F) evince two

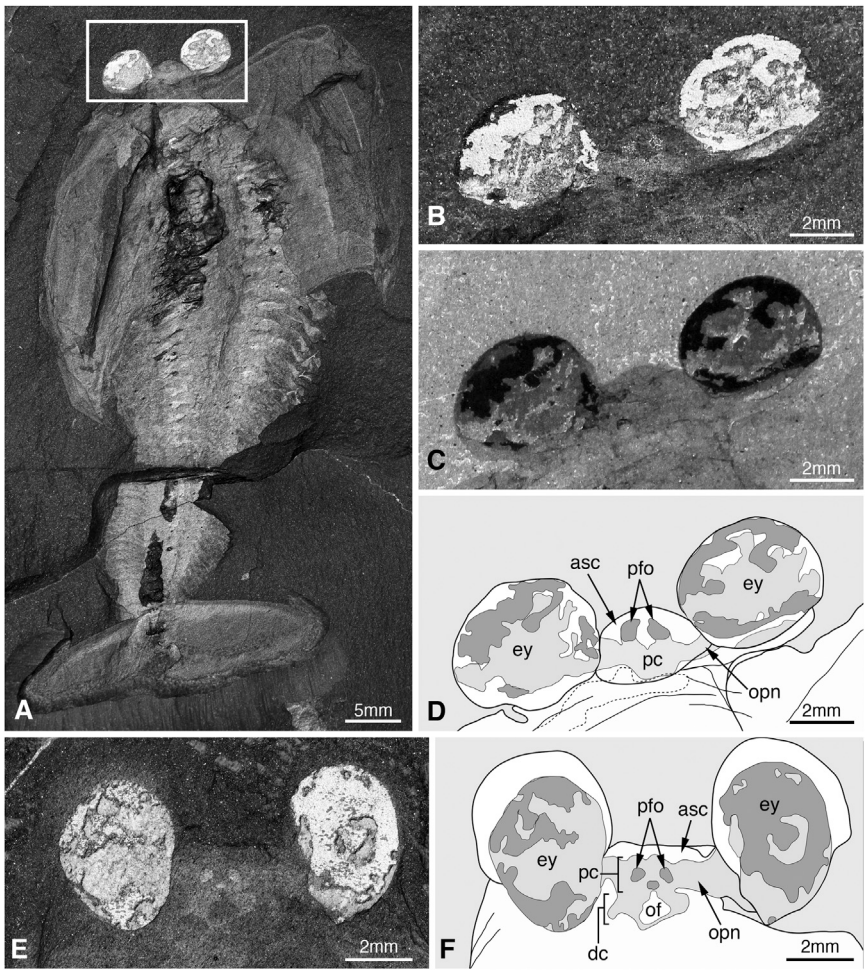

Figure 2. Protocerebral Structures in *Odaraia alata*

(A–D) ROM 60746 in ventral view (courtesy of J.B. Caron, ROM, and Parks Canada).

(A) Complete specimen (cross-polarized high angle illumination, dry). White box indicates location of magnified area in (B)–(D).

(B) Detail of anterior cephalic structures (cross-polarized high angle illumination, dry).

(C) Detail of anterior cephalic structures (cross-polarized high angle illumination, wet).

(D) Interpretative line drawing of ROM 60746. Grayscale indicates different styles of preservation: white, non-reflective cuticle; light gray, mildly reflective neurological structures; dark gray, highly reflective neurological structures. Dotted lines indicate non-biological fissures. Note that the morphology of the optic nerve (*opn*) reflects that of the eyestalk, and thus only the former is labeled in the figure.

(E) Detail of anterior cephalic structures in USNM 189232, dorsal view (cross-polarized high-angle illumination, dry).

(F) Interpretative line drawing of USNM 189232.

Other abbreviations used: *asc*, anterior sclerite; dc, deutocerebrum; *ey*, eyes; *of*, esophageal foramen; *opn*, optic nerve; *pc*, protocerebrum; *pfo*, protocerebral frontal organ.

well-defined, small (~15%–20% anterior sclerite, transverse and sagittal) frontal organs positioned close to the sagittal plane of the anterior sclerite (see *pfo* in Figures 2D, 2F, and 4C; see also Figures S3 and S4). A third—slightly smaller—frontal organ is located posteriorly in the midline of USNM 189232 (Figures 2E and 2F; see also Figure S4); this frontal organ is not observed in ROM 60746, likely due to its ventral preservation. ROM 60746 indicates that each of the paired frontal organs bears a stub-like peduncle that directly connects anteromedially to a substantial mass of reflective material occupying most of the area within the anterior sclerite (*pc* in Figure 4D); the peduncles are not observable in USNM 189232 due to differences in orientation, as the frontal organs are preserved directly on top of the reflective mass rather than extended forward relative to the former (as in ROM 60746). The reflective mass is bilaterally symmetrical, consisting of a sagittal anterior depression flanked by lobe-like swellings with direct connections to the lateral eyes (Figures 2B and 2D; see also Figures S3A and S3B). USNM 189232 demonstrates that the reflective mass bifurcates into two posterior swellings (*dc* in Figures 2E and 2F) extending toward the trunk and leaving a distinctive gap medially (*of* in Figures 2E and 2F; see also Figure S4); the posterior swellings and the associated gap are not preserved in ROM 60746.

Similarly to *H. expansa*, the frontal organs of *O. alata* are regarded as median eyes [8, 45] by comparisons with similar structures in numerous extant euarthropods [33, 34, 37, 41, 42] (Figures 4E and 4F). The continuity between the frontal organs and the stalked lateral eyes, through the reflective mass in the anterior sclerite of *O. alata*, support this interpretation. The lobe-like structure and bilateral symmetry of the reflective mass fall within the neurological diversity reported for early Cambrian total-group euarthropods [4–6, 25], bearing the closest similarity with the bilobed brain of the upper stem euarthropod *Fuxianhuia protensa* [4]; the frontal organ triplet and general brain outline also show parallels with those of *Waptia fieldensis* [39] and extant mandibulates [46] (Figure 4). The anterior swellings and connections with the stalked lateral eyes are interpreted as protocerebral lobes and the optic nerves respectively (*pc* and *opn* in Figures 2D and 2F; see also Figures S2C–S2F); individual neuropils are not preserved. The position of the frontal organs indicates an origin close to the anterior midline of the protocerebrum, probably to a region homologous with the arcuate body or central complex of extant Euarthropoda [33, 37]. The location of the paired posterior swellings indicates that they represent the deutocerebrum (*dc* in Figures 2F and 4C) and that the resulting medial gap corresponds to the esophageal foramen (*of* in Figures 2E, 2F, and 4C). There is no clear evidence of nerves extending to the body appendages, possibly reflecting the apparent absence of cephalic limbs—including antennae—in *O. alata* [8, 45]. The organization of the anterior brain and its constituent structures indicates that the frontal organs and anterior sclerite of *O. alata* are also associated with the protocerebral segment.

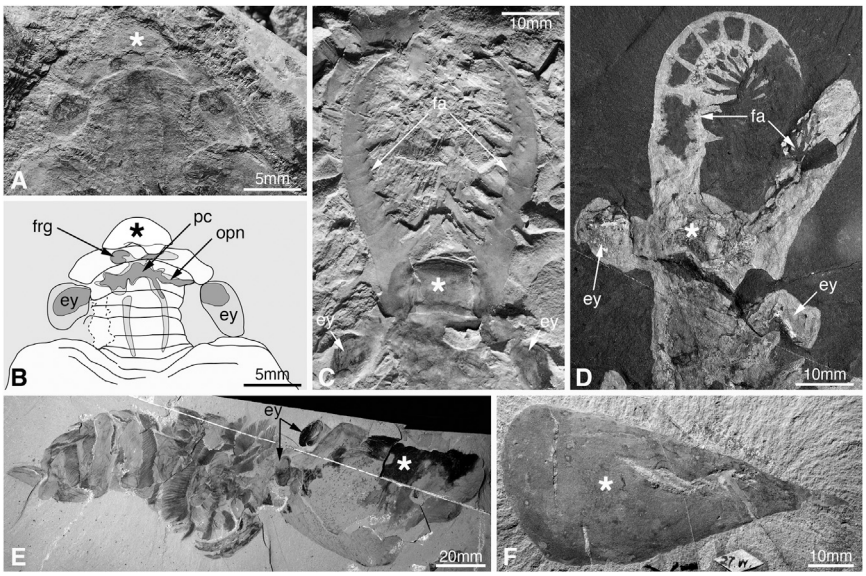

Figure 3. Protocerebral Cephalic Sclerites in Early and Middle Cambrian Radiodonta

(A) *Lyrarapax unguispinus* (YKLP 13305; courtesy of P. Cong, Yunnan University).

(B) Interpretative drawing of YKLP 13305. Gray-scale indicates different styles of preservation: white, body cuticle; light gray, mildly preserved neurological structures; dark gray, well-preserved neurological structures. Dotted lines indicate non-biological fissures.

(C) *Anomalocaris saron* (ELRC 20001; courtesy of G.D. Edgecombe, Natural History Museum, UK).

(D) *Anomalocaris canadensis* (ROM 51212; courtesy of J.B. Caron, ROM, and Parks Canada).

(E) *Hurdia victoria* (USNM 274159; courtesy of A.C. Daley, University of Oxford).

(F) Isolated "H-element" of *Hurdia victoria* (USNM 57718, holotype; courtesy of A.C. Daley, University of Oxford).

Abbreviations used: *ey*, eye; *fa*, frontal appendage; *frg*, frontal appendage ganglion; *pc*, protocerebrum; *opn*, optic nerve. Dorsal plate is marked by asterisk.

Origin of the Anterior Sclerite

The morphology and organization of protocerebral non-appendicular exoskeletal structures in the head region of *H. expansa* and *O. alata* support the homology of the anterior sclerite across phylogenetically distant total-group euarthropods (Figures 3 and 4; Table S2). This conclusion can be extended to fossil taxa that share a similar anterior architecture, namely fuxianhuiids [4, 7, 22–25], bivalved upper stem-group euarthropods [8, 26, 27], and artiopodans [20, 21, 23, 28, 31] (Figure 4). It is also reasonable to infer a protocerebral association in cases where the sessile frontal organs are located in front of the hypostome/labrum complex, even in the absence of a discrete anterior sclerite (e.g., *Agnostus pisiformis* [47] and *Sinoburius lunaris* [19, 23]; see Table S2). By contrast, the homology between the frontal organs of Paleozoic euarthropods (Table S2) and median eyes of extant representatives [33, 34, 37, 41] is less resolved. The frontal organs of *H. expansa* and *O. alata* lack fine morphological details, and thus it is uncertain whether their developmental is similar to the median eyes of either Chelicerata [5, 33] or Mandibulata [4, 37, 41] based on the presence of optic neuropils. However, these findings lead to a more significant comparison with the cephalic organization of lower stem-group euarthropods [1]. In addition to the pair of pre-ocular frontal appendages (*fa* in Figures 3C and 3D; see Supplemental Discussion), radiodontan species known from complete specimens possess a dorsal exoskeletal plate (asterisk in Figure 3) associated with the attachment site of the lateral stalked eyes, and that overlies the proximal bases of the raptorial limbs [6, 9, 10, 17, 18, 32, 48, 49] (Figures 3C and 3D). The dorsal plate has a subcircular outline and is generally confined to the cephalic margins in *Anomalocaris* (Figures 3A–3D) [9, 17, 18], but it can also be drastically modified as exemplified by the dorsal "H-element" of hurdiids [10, 32, 48, 49] (Figures 3E and 3F). Despite this variability, the recent description of the brain structure in the early Cambrian *Lyrarapax unguispinus* [6] draws attention to a fundamental correspondence between the radiodontan dorsal plate and the euarthropod anterior sclerite. The organization of the neurological tissues preserved in *L. unguispinus* resemble those of *H. expansa* and *O. alata* in their bilateral symmetry, direct connections to the stalked lateral eyes, and presence of paired structures emerging from the anterior edge of the brain that occupy a position close to the median region (Figures 3A and 3B). A critical difference is that the paired structures on the anterior brain of *L. unguispinus* correspond not to frontal organs, but rather to ganglia that innervate the frontal appendages (*frg* in Figure 3B) [6]. This similarity should not be taken to imply the primary homology between the frontal organs in *H. expansa* and *O. alata* with the frontal appendage ganglia of *L. unguispinus*, however, as these structures have different developmental origins as visual organs and limbs, respectively. As in other radiodontans [9, 10, 17, 18, 32, 49], the cephalic region of *L. unguispinus* bears a subcircular dorsal plate associated with the stalked lateral eyes [6] (asterisk in Figures 3A and 3B). Given that the radiodontan dorsal plate overlies all of the neurological structures emerging from the anterior region of the brain and the bases of the lateral eyes (Figures 3A and 3B), it is concluded that this isolated sclerite has an association with the protocerebral segment.

The anterior sclerite in *H. expansa* and *O. alata* evinces morphological, topological, and neurological similarities with the dorsal plate of radiodontans, indicating that these cephalic exoskeletal structures share a common origin as derivatives of the protocerebral segment (Figure 4). This comparison clarifies previous disagreements over the homology of the anterior sclerite [8–10, 19, 21, 22, 24, 25, 28, 30–32, 49] (Table S1), particularly across the evolutionary transition from taxa with a lobopodian-type construction (lower stem Euarthropoda) to completely sclerotized forms with fully arthrodized bodies and arthropodized appendages (Deuteropoda [1]). The anterior sclerite represents the only non-appendicular exoskeletal feature that directly links the cephalic organization of radiodontans (i.e., one-segmented head with pre-ocular first appendages [2, 6]) with that of fuxianhuiids, bivalved forms, and artiopodans (i.e., multisegmented head with deutocerebral

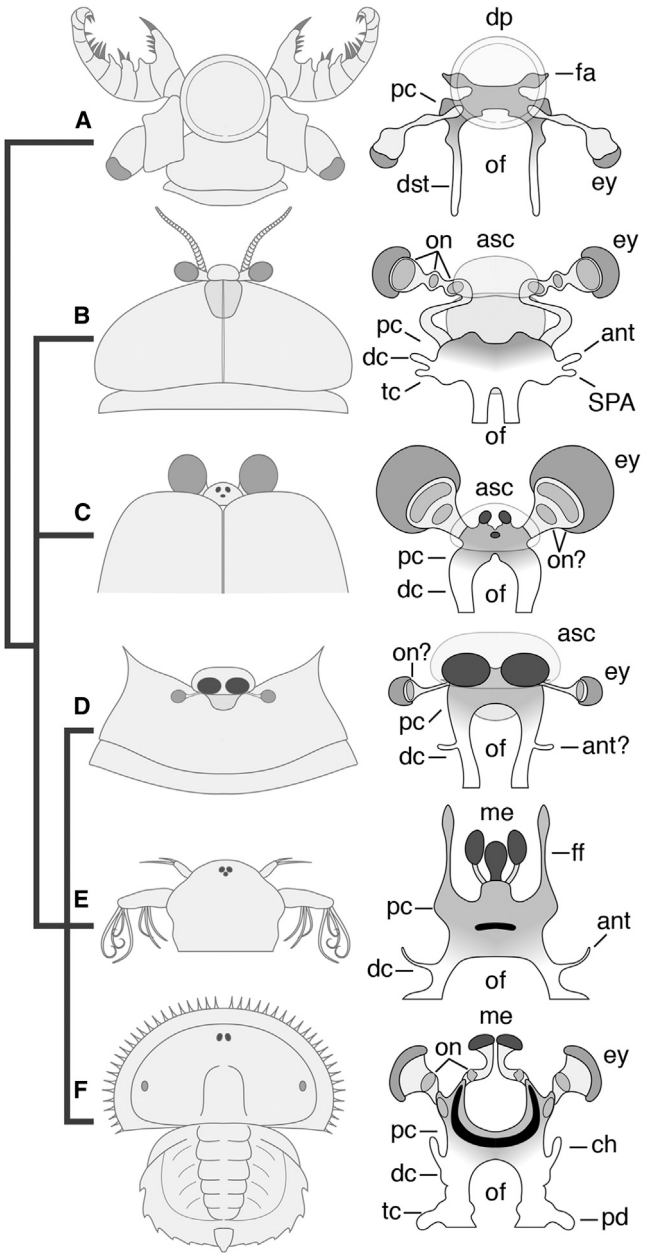

Figure 4. Exoskeletal and Neurological Organization of the Protocerebral Segment in Total-Group Euarthropoda

Tree topology follows [1]. The correspondence between the protocerebrum (*pc*), lateral stalked eyes (*ey*), and median eyes/frontal organs (dark gray) supports the homology of the dorsal plate (*dp*) of radiodontans (A) with the anterior sclerite (*asc*) of upper stem-group (B and C) and crown-group (D) euarthropods as derivates of the protocerebral segment; the anterior sclerite is lost in extant mandibulates (E) and chelicerates (F). Note that the presence of optic neuropils (*on*) in the median eyes of chelicerates (F) (e.g., [33]) argues against their homology with the neuropil-less median eyes of mandibulates (E) despite their similar position on the body (e.g., [34]). The presence of the arcuate body/central complex (black) in the protocerebrum of fossil taxa (A)–(D) is unknown.

(A) *Lyrarapax unguispinus*, cf. [6].

(B) *Fuxianhuia protensa*, cf. [4]. The ventral hypostome is highlighted (light gray). Neurological reconstruction slightly modified from Ma et al. [4].

(C) *Odaraia alata*. Presence and organization of optic neuropils in lateral eyes are hypothetical.

(D) *Helmetia expansa*. Brain morphology and presence and organization of optic neuropils in lateral eyes are hypothetical. The ventral hypostome is highlighted (light gray).

(E) *Triops cancriformis* nauplius, cf. [34]. Note that *T. cancriformis* lacks stalked lateral eyes.

(F) *Limulus polyphemus* "trilobite stage," cf. [33].

Other abbreviations used: *ant*, antenna; *ch*, chelicera; *dc*, deutocerebrum; *dst*, descending tract (cf. [6]); *fa*, frontal appendage; *ff*, frontal filament; *of*, esophageal foramen; *pd*, pedipalp; *SPA*, specialized post-antennal appendage; *tc*, tritocerebrum.

first appendages [1, 4, 7, 12]) (Figure 4). Although the lateral "P-elements" of hurdiids [9, 10, 48, 49] are most likely also associated with the protocerebral segment based on their anterior position on the body, these accessory sclerites represent phylogenetically derived features within Radiodonta [6, 49] and thus have no direct relationship with the origins of the euarthropod anterior sclerite. The persistence of the anterior sclerite in upper stem euarthropods suggests that some protocerebral components were relatively unaffected by the segmental reorganization involved in the origin of the multisegmented euarthropod head. This transformation resulted in the reduction of the radiodontan frontal appendages into the hypostome/labrum complex covering the posterior-facing mouth opening [2, 3, 6, 8, 26] and the co-option of the deutocerebral appendages as the antenniform first limb pair of Deuteropoda [1, 4, 7, 12, 19, 22–25, 27, 28, 30, 31]. The changes in the segmental architecture of the anterior region also involved subtle differences in the cephalic organization between lower and upper stem Euarthropoda; for instance, the radiodontan dorsal plate changed from having a broad attachment to the body (e.g., Figures 3 and 4A) to the more forward-positioned and free-hanging anterior sclerite of upper stem euarthropods (Figures 1B–1D, 2B–2D, and 4B–4D).

The anterior sclerite has a deeper origin within the euarthropod stem lineage than previously considered, and therefore the widespread distribution of this character among Paleozoic representatives is ancestral (per [8], contra [20]). The absence of an anterior sclerite in most crown-group euarthropods represents a derived condition (Figures 4E and 4F), likely resulting from the fusion of the latter structure with other constituents of the cephalic exoskeleton [19, 21, 25]. This conclusion impacts the formulation of phylogenetic analyses of total-group Euarthropoda, as most previous studies have not adequately reflected the homology and protocerebral origin of the dorsal plate/anterior sclerite among Paleozoic representatives, or have inadvertently over-split this relationship into separate characters (see Table S1). The integration of paleoneurological and developmental data into cladistics-based tree reconstructions [3] is crucial for resolving the phylogenetic relationships within total-group Euarthropoda and thus leads to an improved understanding of the origins and complex evolutionary history of this successful group.

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures, two tables, and Supplemental Discussion and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.04.034.

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